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Radial growth responses of tulip poplar (*Liriodendron tulipifera*) to climate in the eastern United States

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Abstract. Tulip poplar is an important component of the eastern deciduous forest and one of the few diffuse-porous tree species with indeterminate apical growth in North America for which there are substantial dendroecological data. This dendroecological study evaluated correlations between radial growth of tulip poplar and monthly, seasonal, and annual climate variables and how these correlations varied across time and spatial climate gradients. The strongest and most spatially consistent correlations were with climate variables related to site water balance, especially precipitation. Growth was positively correlated with climate variables related to site water balance during the months of May through July of the year the annual ring forms and during the previous year growing season and autumn. Growth was negatively correlated with prior year growing season maximum temperature, but positively correlated with prior winter minimum temperature. There was some evidence of temporal variation in growth–climate associations between 1900 and 2016, but the climate variables with the strongest associations were consistent across different time periods. Correlations with climate variables related to water stress increased from east to west as precipitation decreased, but there was no spatial trend in correlations with growing season temperature from north to south as temperature increases. Strength of positive correlations with winter temperature increased from north to south. Growth of tulip poplar will likely be adversely affected if drought frequency or severity increases during the twenty-first century. Increased winter temperature would likely have a positive influence on growth during the subsequent growing season in some parts of the species range. Radial growth of tulip poplar is most affected by climate conditions during a narrow time period early in the growing season, similar to results obtained for multiple oak species and a few other diffuse-porous species in eastern North America. Simulation modelers might consider the phenology of these correlations to formulate more biologically realistic tree climate response functions.

Key words: climate response; dendroecology; diffuse porous; spatial variation; temporal variation.

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INTRODUCTION

The dominant natural vegetation in the eastern United States is deciduous forest, including a great diversity of angiosperm tree species and some conifer species (Currie and Paquin 1987, Dyer 2006). The moist-temperate forests of this region provide important wildlife habitat and ecosystem services, and are a major source of raw material for various industries. Mature moist-temperate forests such as these also have some of the highest carbon stores of any forest type in the world (Keith et al. 2009). The ability of these forests to act as a carbon sink could be reduced if climate change results in reduced tree growth (Charney et al. 2016), or they could become a source of CO_2 emissions in the future if climate change results in widespread tree mortality (Allen 2010, Anderegg et al. 2013, Williams 2013, Allen et al. 2015, Anderegg 2015).

Climate projections for the twenty-first century in the eastern United States indicate that growing season temperature will increase, precipitation may slightly increase or decrease (depending on region), and surface soil water availability will decrease due to increased evapotranspiration (USGCRP 2017). Drought frequency and intensity are projected to increase due to increased evapotranspiration (Cook et al. 2014, USGCRP 2017). More rainfall is projected to occur in intense precipitation events (USGCRP 2017), during which a greater proportion may be lost to surface runoff rather than infiltrating into the soil water reservoir. Given the importance of forests in the eastern United States, it is critical to understand the potential effects of these changes in climate on these ecosystems.

The changes in climate described above are projected to occur within the lifespan of many existing mature trees. The vast majority of dendroecological studies done in eastern North America have shown that drought stress reduces tree radial growth (LeBlanc and Terrell 2009, 2011, Pederson et al. 2012*a*, *b*, LeBlanc and Stahle 2015, Martin-Benito and Pederson 2015, Maxwell et al. 2016, D'Orangeville 2018, LeBlanc and Berland 2019). Studies in other regions have also linked severe heat and drought events to widespread tree mortality (Allen 2010, Anderegg et al. 2013, Williams 2013, Allen et al. 2015, Anderegg 2015). A global study of forest vulnerability to drought found that 76% of tree species evaluated from 81 sites worldwide had a narrow safety margin for hydraulic failure due to drought stress (Choat 2012). This vulnerability was largely independent of current precipitation, suggesting that all forest biomes may be vulnerable to drought-induced growth decline and mortality, including the relatively mesic eastern deciduous forest. Adams et al. (2017) showed that higher temperature resulted in greater mortality associated with droughts. In addition, drought stress can render trees more susceptible to pests and pathogens, causing additional tree mortality (Manion 1990, Wood et al. 2018). However, the effects of drought on tree growth and mortality may vary among different species (Cook et al. 2001, Fan et al. 2012).

Dendroecological analyses provide one approach for assessing the sensitivity of tree species on particular sites to climate stresses by studying correlations between historical fluctuations in climate and variation in tree radial growth. Spatially replicated, strong correlations between tree-ring width and climate variables indicate tree species and site types for which climate is an important limiting factor to growth (LeBlanc and Stahle 2015, Martin-Benito and Pederson 2015, D'Orangeville 2018). Growth–climate correlation analyses that use monthly and seasonal climate variables enable identification of specific periods during the year when tree species are more or less sensitive to climate stressors. Forest simulation models that incorporate such ecophysiological information could provide more realistic predictions of climate change impacts on tree species and forests.

Most dendroecological studies have focused on conifer species in cold or semi-arid environments (Zhao et al. 2018). Studies of hardwoods in the eastern United States have focused predominantly on ring-porous oak (*Quercus)* species (LeBlanc and Terrell 2009, 2011, LeBlanc and Stahle 2015, Martin-Benito and Pederson 2015). A search of the International Tree-Ring Data Bank (ITRDB) in 2018 identified only 23 chronologies for diffuse-porous tree species from this region. If dendroecological studies of tree growth–climate correlations are to be useful for projecting forest response to future climate change in the species-rich eastern deciduous forest of North America, a wider sampling of tree species will be necessary (Alexander et al. 2019).

Tulip poplar (*Liriodendron tulipifera* L.) has diffuse-porous wood anatomy and indeterminate apical growth and differs in many ways from more widely studied oak species that have ring-porous wood and determinate apical growth (Zimmerman and Brown 1971:47). The indeterminate pattern of continued growth into the latter months of the growing season may cause this species to be more susceptible to late summer droughts than oaks, which have mostly ceased shoot growth after July. The biological and ecological differences between tulip poplar and the more widely studied eastern oak species provide an opportunity to explore the diversity of tree growth responses to climate in the eastern United States.

Tulip poplar is an economically important, fast-growing pioneer species found throughout much of the eastern deciduous forest (Burns and Honkala 1990). This species is characterized as site-sensitive, meaning that it is most commonly found on high-quality mesic sites. Canham and Thomas (2010) found that tulip poplar had the narrowest niche breadth of any of the 24 common tree species in their analysis of forests in the eastern United States, with the greatest frequency of occurrence at sites with warm average annual temperatures and moderate rainfall. The narrow habitat requirements for this species could render mature trees susceptible to future changes in climate conditions. Previous studies have demonstrated that tulip polar was sensitive to variation in climate conditions (Martin-Benito and Pederson 2015, Maxwell et al. 2015, Maxwell and Harley 2017, Helcoski et al. 2019).

A multispecies study of tree growth–climate correlations in the eastern United States by Martin-Benito and Pederson (2015) included 15 sites where tulip poplar was sampled, but the vast majority of these sites were located east of the Appalachian Mountains. A large-scale spatial analysis of oak growth–climate associations in eastern North America indicated that trees at sites east of the Appalachians were less affected by drought stress than trees at sites west of this mountain range; this spatial variation was associated with a climate gradient of decreasing precipitation from east to west (LeBlanc and Berland 2019). The study presented here includes the data from Martin-Benito and Pederson (2015) and adds data from 30 more sites, most of which are located in the drier region west of the Appalachians (McLaughlin et al. 1986, Maxwell and Harley 2017). This allows for an analysis of variation in growth–climate correlations along both latitudinal and longitudinal climate gradients. Hence, the analyses presented in this paper constitute a significant addition to current understanding of tree growth responses to climate stresses in the eastern United States.

The goal of this study was to characterize tulip poplar radial growth responses to variation in climate conditions and to evaluate spatial and temporal variation in strength of these associations across geographic climate gradients. First, we identified associations between radial growth of tulip poplar and climate variables that are likely to reflect cause–effect relationships. For those climate variables that had the strongest evidence for a cause–effect relationship with radial growth, we evaluated spatial and temporal variation in the strength of growth–climate associations across substantial climate gradients to test the following hypotheses: (1) Strength and spatial consistency of correlations between radial growth and site water balance variables will increase from southeast to northwest along a gradient of decreasing precipitation, (2) strength and spatial consistency of correlations between radial growth and summer maximum temperature will increase from north to south along a latitudinal gradient of increasing temperature, and (3) the strength of growth–climate associations will vary over time at locations where climate conditions have varied, increasing where climate has become more stressful and vice versa.

METHODS

Sources of tree-ring data

Tree-ring data used in this study were obtained from several sources. The FORAST study (McLaughlin et al. 1986) attempted to obtain a data from representative samples of overstory trees from a large number of sites distributed across the eastern half of the United States, excluding trees that were either obviously damaged or that had experienced substantial release from competition in recent years. Most of the sites sampled for the FORAST study were second-growth forests where overstory trees were mostly less than 100 yr old. Most of the other data used for the current study were obtained for paleoclimate reconstruction of historical climate. Sampling for such studies generally focuses on canopy trees in forests believed to contain old trees to obtain the longest possible tree-ring chronologies. Most of these data collections were developed by the authors of this study or obtained from the ITRDB in 2018. Pederson et al. (2012*a*, *b*) compared growth–climate correlations between chronologies developed from selectively sampled trees in old-growth forests and those from nearby randomly sampled second-growth forests and found only small differences. Hence, this analysis combined data from these various sources to obtain a sufficiently large data set to evaluate spatial variation in growth–climate correlations of tulip poplar across climate gradients in the eastern United States (Fig. 1).

Tree-ring chronology development

Increment cores from newly collected sites were visually cross-dated to assign each annual ring to the calendar year it was formed. Tree-ring widths were measured to 0.001-mm precision. Cross-dating and measurement data quality were evaluated using the program COFECHA (Holmes 1983). Cross-dating of tree-ring data downloaded from the ITRDB and previously published data was also verified.

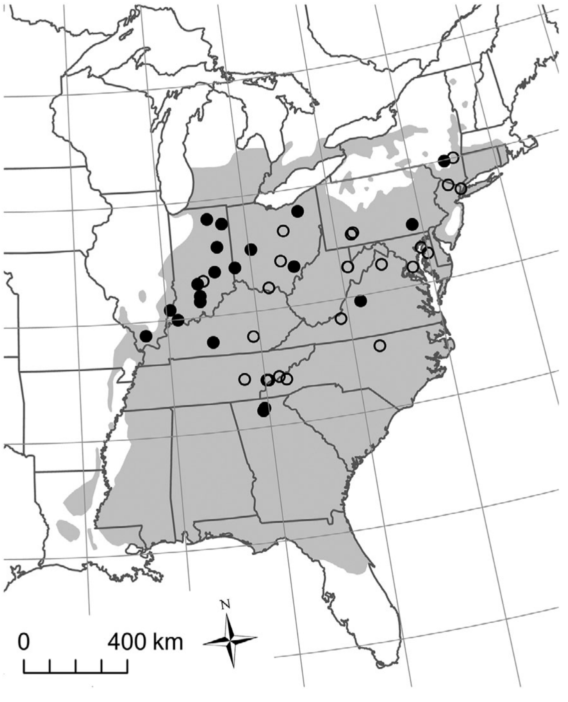

Fig. 1. Map of site locations where tulip poplar was sampled within the range of the species in eastern North America (gray shaded area). Filled circles indicate sites where the tree-ring chronology was sufficiently long to justify analysis of temporal variation in growth–climate associations.

Ring width chronologies for individual cores were processed using ARSTAN (Cook 1985) to produce a mean tree-ring index chronology for each site. A 50-yr smoothing spline was used to remove long-term trend, and temporal autocorrelation was removed from each individual core chronology. The 50-yr spline was chosen to facilitate comparisons with a large oak dendroecological database (LeBlanc and Terrell 2009, 2011, LeBlanc and Stahle 2015, LeBlanc and Berland 2019). A robust bi-weight mean was used to average by year the index chronologies for 8–22 trees sampled from a site to produce a residual (RES) tree-ring index chronology for each site.

Climate data

Data for monthly mean temperature (T), maximum temperature (MxT), minimum temperature (MnT), precipitation (P), and Palmer drought severity index (PDSI, sometimes abbreviated to D for variable names) for the eastern United States were obtained from the National Climate Data Center (NCDC 2018). Data values were averages for weather recording stations within state climate divisions (SCDs). Mean monthly temperature and precipitation data were used to calculate potential evapotranspiration (PE) and actual evapotranspiration (AE) using a modified Thornthwaite-Mather algorithm (LeBlanc and Terrell 2001). Site water balance was evaluated by the ratio of precipitation to potential evapotranspiration (P:PE) and the ratio of actual to potential evapotranspiration to potential evapotranspiration (AE:PE). Monthly climate data were used to compute seasonal climate variables for prior summer (pSm, June–August of the year prior to annual ring formation), prior autumn (pAt, September–November), prior winter (pWn, December–February), spring (Spr, March–April), and early growing season (Sm, May–July of the year the annual ring formed).

Analyses of radial growth–climate associations

Pearson's product–moment correlations were computed for the association between tulip poplar residual chronologies and the monthly and seasonal climate variables described above. Variables included monthly climate variables for June of the year before annual ring formation through September of the year the annual ring formed and the seasonal climate variables described above. Correlations were also computed for annual climate variables, based on data for prior June through current year September. We chose this time span for annual variables because it combines the lagged effects of prior growing season conditions with direct effects of current growing season conditions.

The analysis of growth–climate correlations involved a large number of climate variables, each with its own correlation coefficient and test of significance. With a nominal type I error rate of $\alpha = 0.05$ applied to the correlation analysis for each climate variable, there was a high probability of identifying apparently significant correlations that were attributable to random chance. In this study, we focused on those climate variables that were significantly correlated ($P \leq 0.05$) with radial growth indices at 7 or more of the 45 sites. Based on a binomial distribution ($n = 45$, $P = 0.05$), if $X = 7$ or more out of $n = 45$ sites had a significant correlation with one of the monthly variables, the overall type 1 error rate for that climate variable would be $\leq$0.05.

When growth is strongly correlated with one climate variable, this can sometimes obscure associations with other climate variables in a simple univariate correlation analysis. Seasonal climate variables that met the spatial replication criterion described above were entered into a forward selection stepwise regression model. An initial analysis that included all seasonal variables that met the spatial replication criterion revealed substantial multicollinearity among the growing season variables for P, MxT, PDSI, and P:PE. Since the variables PDSI and P:PE are computed from precipitation and temperature, the regression analysis was performed using only the simpler P and MxT variables. A significance level $P \leq 0.05$ was required for variables to enter and be retained in the regression model.

Paired *t*-tests (by site) were used to compare the strength of growth–climate correlations between different climate variables. While Pearson's product–moment correlations are not normally distributed, the sample size of $n = 45$ sites allowed for the central limit theorem to apply. Therefore, the sampling distribution for the mean of the paired differences could be assumed normal. Hence, the correlation coefficients were not transformed, allowing the mean of the paired differences to be more easily interpretable.

Selection of climate variables

Because this study included 154 climate variables (7 different variables for 22 months or seasons), the first step in the analyses was to determine which climate variables were best associated with radial growth of tulip poplar so that further analyses could focus on a smaller number of variables. Evaluation of climate variables was based on spatial replication of correlations among the 45 study sites and the mean strength of statistically significant correlations. This evaluation was based on all available data for each of the sites.

The strongest and most spatially replicated growth–climate correlations were with climate variables for the months May–July of the current year when the annual ring was formed (Appendix S1: Figs. S1, S2). There was little evidence that radial growth of tulip poplar was affected by growing season climate conditions after July of the current year. Climate variables for prior year late summer, autumn, and winter months were also correlated with growth of tulip poplar.

The strength and spatial replication of growth–climate correlations were generally similar or stronger for seasonal climate variables compared to correlations with monthly climate variables (Appendix S1: Figs. S1, S2). Hence, only correlations with the smaller number of seasonal variables were included in further analyses of temporal and spatial variation in growth–climate associations. Correlations with growing season temperature were more spatially replicated for maximum temperature variables compared with mean and minimum temperature variables (Appendix S1: Fig. S2). Correlations with prior winter temperature were more spatially replicated for mean and minimum temperature variables than maximum temperature.

Correlations with annual site water balance variables (precipitation, PDSI, P:PE) were somewhat weaker than correlations with monthly and seasonal variables, but had similar spatial replication (Appendix S1: Fig. S1). Correlations with annual temperature variables were generally weaker and not as spatially replicated as correlations with monthly and seasonal variables (Appendix S1: Fig. S2).

On average, correlations with precipitation, PDSI, and P:PE had similar strength and spatial replication as correlations with the more complex variables actual evapotranspiration and AE:PE ratio (Appendix S1: Fig. S1). Therefore, only correlations for the simpler precipitation, PDSI, and P:PE variables were included in further analyses.

Temporal variation in climate and growth–climate associations

Because the database of 45 sites included chronologies that differed with regard to the span of years included, the next question that had to be addressed was whether the results of growth–climate correlation analyses exhibit temporal variation.

Temporal variation in those climate variables that were most consistently correlated with tulip poplar radial growth was evaluated for each state climate division (SCD) using the slope of a linear best fit line fit to the climate data, with chronological year as the X-axis variable. Linear trends were computed for three time periods: the full period of the data (1900–2017), the period 1930–1980 for which all sites had tree-ring data, and the period 1981–2017.

This analysis identified only modest trends in climate variables across the full period of data (1900–2017), but much stronger trends over shorter periods (Appendix S1: Fig. S3). Early growing season precipitation and PDSI exhibited positive trends over the entire period of record (Appendix S1: Fig. S3A, B). In contrast, summer maximum temperature and winter minimum temperature exhibited strong declining trends from 1930 to 1980, which then reversed to positive trends from 1981 to 2017 (Appendix S1: Fig. S3C, D). The strength and duration of the post-1980 increasing trend were not sufficient to cancel the amount of decline in temperature observed over the 1930–1980 period. Across all 16 state climate divisions included in this analysis, 76% of the top ten highest SmMxT values occurred prior to 1981 and 51% of these hottest years occurring during the common period 1930–1980.

To evaluate whether the results of growth–climate correlation analyses varied over these same three time periods, growth–climate correlations were computed for the full period of data for each site, for just the period 1930–1980 common to all sites, and for the period after 1980. Only 21 sites had sufficient tree-ring data for years after 1980 to be included in the latter analysis.

While there was some evidence of temporal variation in growth–climate correlations, the main results regarding which climate variables were best associated with radial growth of tulip poplar were similar across different time periods (Appendix S1: Figs. S1, S2, S4). Correlations with current growing season SmP, SmD, and SmMxT had better spatial replication than all other climate variables for all three time periods, but correlations with PDSI were less spatially replicated during the period after 1980 (Appendix S1: Figs. S1, S4). Also, correlations with PDSI for months other than the earlier growing season were not significant during the post-1980 period, but were significant during the pre-1980 period.

The specific months when spatial replication of correlations was greatest varied somewhat between periods before and after 1980. Correlations with August precipitation were significant during the 1981–2017 period, but not the pre-1980 period (Appendix S1: Figs. S1, S4). Correlations with MxT were strongest for the May–July period during 1930–1980 ($r = -0.45$), but after 1980 correlations with MxT were stronger for the June–August period ($r = -0.48$) and were not significant for the May–July period (Appendix S1: Figs. S2, S4). Lastly, correlations with maximum temperature during the prior year summer were more spatially replicated for the period after 1980, but correlations with prior growing season and autumn precipitation were better replicated for the 1930–1980 period (Appendix S1: Figs. S1, S2, S4). It is not clear whether these modest differences between time periods reflect changes in actual growth–climate relationships or just random sampling variation between different time periods.

To further examine whether climate–growth associations were time-dependent, we used a state-space model with time-varying parameter regression and the Kalman filter (Kalman 1960). The time-varying method with the Kalman filter has been successfully used by others to examine time dependency of climate–growth relationships (Cook and Johnson 1989, LeBlanc 1993, Visser et al. 2010, Bishop et al. 2015). This analysis was performed for 21 sites for which there was a sufficient tree-ring data for years after 1980. Tree-ring index chronologies were the dependent variable, and climate variables were the independent variables. Only seasonal variables that were correlated with radial growth at ten or more sites were entered in the Kalman filter analysis, including pSmP, SmP, pSmD, SmD, SmMxT, and WnMnT.

While the Kalman filter analyses identified temporal variation in strength of some growth–climate associations, this was not consistently related to temporal trends in climate variables. Temporal variation in growth–climate associations was identified at 11 of the 21 sites included in the analysis, but for only 15 out of a total of 126 site × climate variable combinations evaluated. Coincident with long-term temporal trends of increasing summer precipitation and PDSI, the strength of association between radial growth and these variables became weaker at 7 of the 11 sites analyzed (Appendix S1: Fig. S5). However, the strength of associations with these water balance variables increased over time at 4 sites, in spite of the wetter conditions. At one site, the association with winter minimum temperature became slightly stronger over time, but there was virtually no temporal trend in this climate variable (+0.001°C per yr). Otherwise, there was no evidence of temporal variation in strength of associations with temperature. Taken together, these results do not indicate a consistent pattern of temporal variation in the strength of growth–climate associations that might be related to temporal trends in climate. Hence, all further analyses of growth–climate associations were based on data for the years 1930–1980 that were common to all 45 study sites. This choice was further justified by the need for experimental control in analyses of spatial patterns in growth–climate associations with regard to the time period used to compute growth–climate correlations and climate summary statistics across all sites.

Analysis of spatial variation in growth–climate associations

Analysis of spatial variation in the strength of growth–climate correlations included only those climate variables that met the spatial replication criterion described above. The mean values for each climate variable computed for the period 1930–1980 for each state climate division were used to define spatial climate gradients. LeBlanc and Berland (2019) analyzed the same climate data used for this study and found that long-term mean values for climate variables were strongly correlated with the frequency of years with extreme values that would likely be stressful for trees. This strong correlation between mean values and frequency of stressful years allowed us to focus solely on spatial patterns in the mean values.

We assessed spatial patterns in the strength of the growth–climate correlations using global Moran's *I* (Dale and Fortin 2014). This statistic evaluates the null hypothesis that values are dispersed randomly in geographic space. Moran's *I* value near 0 indicates a random pattern, while positive values approaching 1 indicate spatial clustering such that neighboring sites have similar values. In this case, a significant Moran's *I* result indicating spatial clustering would suggest that the strength of the growth–climate correlation is spatially patterned and that trees at neighboring sites respond similarly to that climate variable. We used a spatial weight matrix based on four nearest neighbors, which resulted in a mean distance of 113 km between neighboring sites. For those variables that exhibited significant spatial clustering, we assessed the nature of spatial variation using Spearman's rank correlation between the strength of growth–climate correlations and site latitude (south to north), longitude (east to west), latitude/longitude (southwest to northeast), and latitude × longitude (southeast to northwest). Spearman's correlation was used instead of Pearson's product moment correlation because the growth–climate correlation values for the 45 study sites were not always normally distributed.

RESULTS

Dendrochronological statistics for the 1930–1980 period common to all sites indicate that tulip poplar is responsive to climate and could be useful for dendroclimatic analyses (Appendix S1: Table S1). While significant temporal autocorrelation was identified at all but one site, for 76% of sites this was a simple first-order process. Mean sensitivity indicated substantial year-to-year variation in ring width (mean for 45 sites was 0.278, range: 0.20–0.384). Mean between-tree correlation (*r*-bar) averaged

0.481, with a range of 0.315–0.662. This indicates that much year-to-year variation in radial growth is shared among the trees sampled at a site.

Radial growth of tulip poplar was positively correlated with early growing season (May–July) site water balance variables at more than 85% of study sites (Fig. 2). The strength and spatial replication of correlations with early growing season precipitation, PDSI, and P:PE were similar. PDSI and P:PE ratio both reflect the balance between precipitation inputs and atmospheric evaporative demand. However, PDSI is a standardized index that reflects annual deviations from long-term average conditions at each site. The P:PE ratio is not standardized and is an absolute measure of the balance between soil water inputs and outputs. For this reason, only correlations with P:PE ratio were analyzed for spatial patterns along climate gradients.

Growth was negatively correlated with early growing season mean and maximum temperature, but positively correlated with minimum temperature (Fig. 2). Negative correlations with SmMxT were more spatially replicated and stronger than correlations with SmT (paired *t*-test, mean difference: 0.069, $P < 0.001$; Fig. 2). Correlations with SmMnT were not as spatially replicated as those with SmT and SmMxT. Positive correlations with SmMnT and negative correlations with SmMxT were mostly spatially

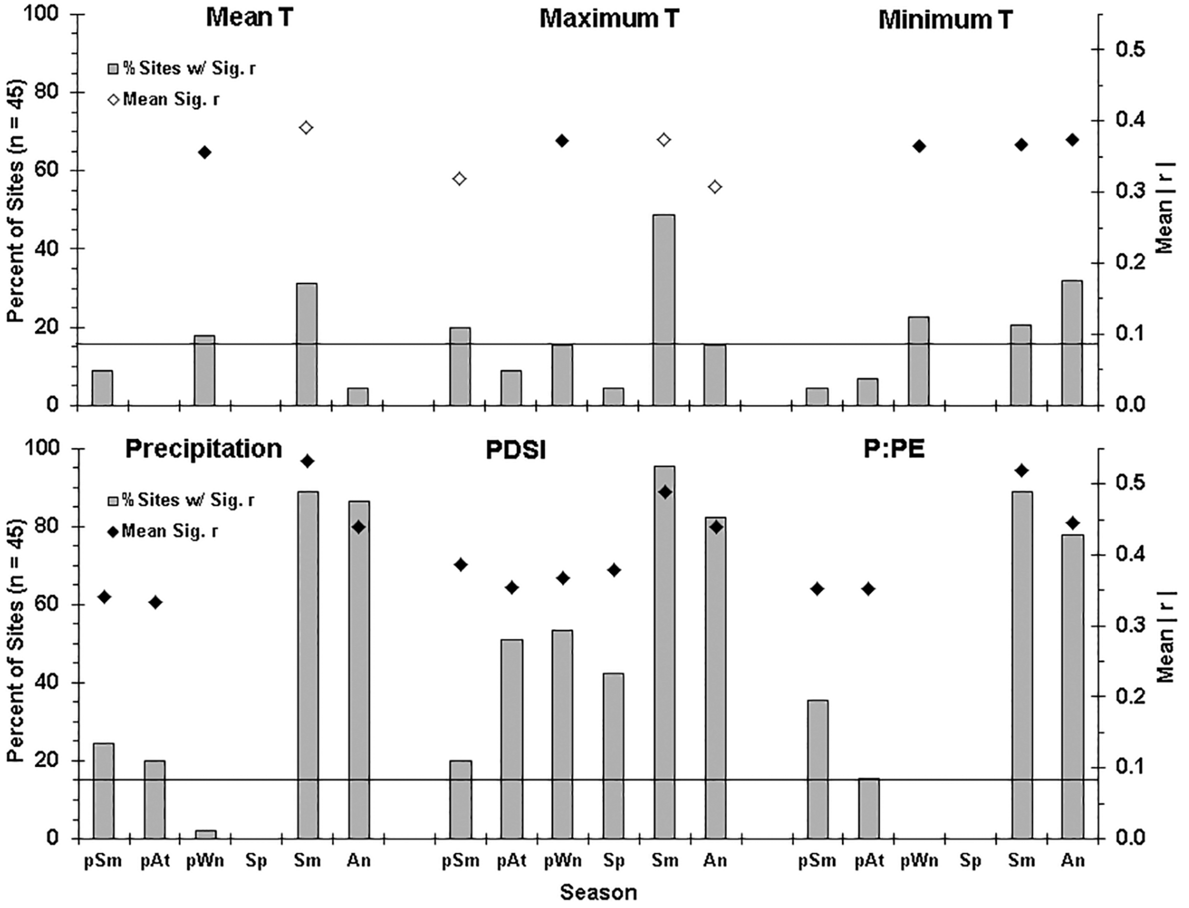

Fig. 2. Growth–climate correlations for seasonal climate variables using data for the common period 1930–1980. Histogram bars represent the percentage of 45 study sites where significant correlations ($P < 0.05$) were observed. Plot symbols indicate the absolute value for the mean of significant correlations, calculated only for those climate variables that had significant correlations at 7 or more sites (indicated by the horizontal line). Filled symbols indicate positive average correlations, and open symbols indicate negative average correlations.

distinct; only two of 45 sites had significant correlations with both of these variables. Positive correlations with SmMnT were observed only at northeastern sites. Negative correlations with SmMxT were observed at most sites west of the Appalachian Mountains and several sites in the east.

Positive associations between growth and early growing season precipitation were stronger and more spatially replicated than negative associations with maximum temperature during the same season. Positive correlations with SmP were observed at 43 of 45 sites, while negative correlations with SmMxT were observed at only 22 sites (Fig. 2). The mean significant correlation with SmP was 0.20 greater than the mean correlation with SmMxT (paired *t*-test, $P < 0.001$). Only at two sites in Tennessee were correlations with SmMxT slightly stronger than correlations with SmP. Current summer precipitation entered multiple regression models as the first or only variable at 37 of 45 study sites, with a positive coefficient and a mean adjusted partial $R^2 = 0.30$ (range: 0.13–0.51; Fig. 3, Appendix S1: Table S2). Summer maximum temperature entered regression models for only 6 sites and failed to attain the spatial replication criterion. Taken together, these results indicate that direct temperature effects on growth of tulip poplar are much weaker than effects of site water balance.

Radial growth was positively correlated with all three temperature variables for the winter prior to the growing season the annual ring was formed (Fig. 2). Average significant correlations were similar among the three different winter temperatures, but correlations with winter minimum temperature were more spatially replicated. Prior winter minimum temperature entered multiple regression models for 17 sites, with a positive coefficient and a mean adjusted partial $R^2 = 0.08$ (range: 0.04–0.18; Appendix S1: Table S2). Of the 10 sites where significant

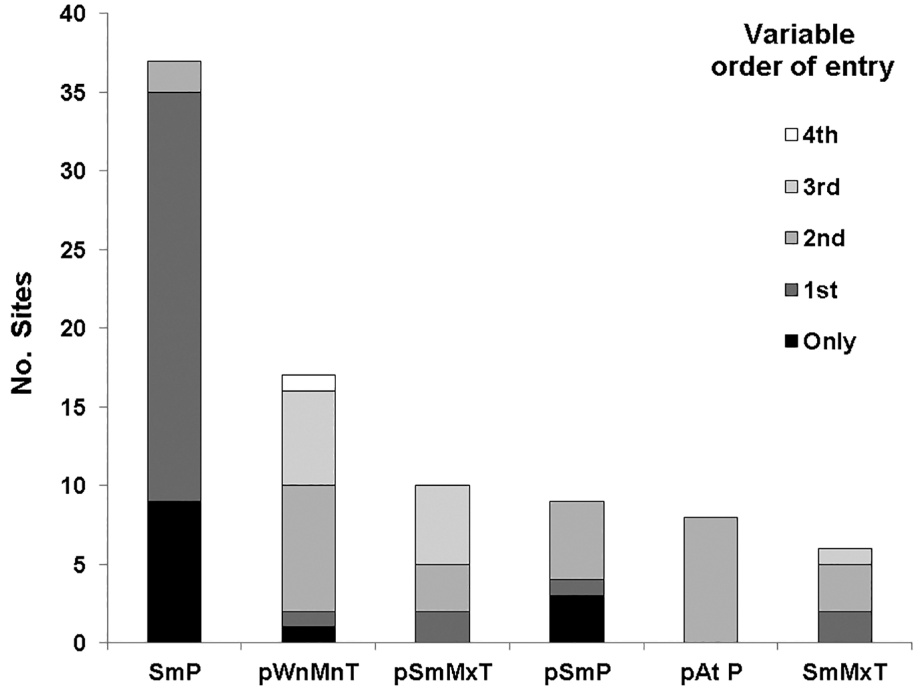

Fig. 3. Order of entry for seasonal climate variables entered into forward selection multiple regression models. The category "Only" indicates that a variable entered as the first and only significant variable to enter the model. The category "1st" indicates that the variable entered first in a multiple variable model. The category "2nd" indicates that the variable entered second in a multiple variable model, and so on. No. sites refers to the number of sites where a variable entered the regression model out of the 45 study sites. See Appendix S1: Table S2 for detailed results from the multiple regression analyses.

correlations with pWnMnT were observed, only 7 retained a significant multiple regression coefficient. However, the regression analysis identified significant positive associations with winter temperature at 10 additional sites where the correlation was not significant.

Growth of tulip poplar was positively correlated with prior growing season and prior autumn precipitation, PDSI, and P:PE and negatively correlated with prior growing season maximum temperature (Fig. 2). However, these correlations with prior growing season climate variables were not as strong or spatially replicated as correlations with corresponding current growing season variables. Prior growing season MxT and P entered regression models at 10 and 9 sites, respectively. These two variables never entered the same regression model, so significant associations with prior growing season climate were identified at a total of 19 sites. Prior autumn precipitation entered regression models for 8 sites, in all cases as the second variable to enter (Appendix S1: Table S2).

Analysis of spatial variation in growth–climate associations

Growth–climate correlations with early growing season climate variables exhibited significant spatial clustering, including correlations with precipitation (Moran's $I = 0.34$, $P < 0.0001$), P:PE ratio ($I = 0.32$, $P = 0.0002$), and maximum temperature ($I = 0.21$, $P = 0.0136$). The strength of positive growth–climate correlations with water balance variables increased from southeast to northwest (SmP $\rho = 0.52$, $P < 0.001$; SmPPE $\rho = 0.47$, $P = 0.001$; Fig. 4A, B). These stronger growth–climate correlations were spatially associated with lower mean SmP and SmPPE (Fig. 5A, B). Three sites in mountainous terrain of West Virginia and North Caroline had moderately strong correlations with SmP and SmPPE, in spite of having the highest values for these water balance variables in our database (Fig. 5A, B). Given their location, this may be due to local soil conditions that restrict soil water-holding capacity, making the trees more dependent on current rainfall. Removal of these outliers had minimal effect on the value of Spearman's rho that quantified the strength of the dose–response association. The strength of negative correlations with SmMxT increased from east to west ($\rho = 0.41$, $P = 0.005$), but was not associated with the latitudinal temperature gradient (Fig. 4C). These stronger negative correlations were spatially associated with higher mean SmMxT (Fig. 5C).

Positive growth–climate correlations with prior year late growing season climate variables related to site water balance exhibited spatial clustering, including correlations with prior autumn precipitation (Moran's $I = 0.51$, $P < 0.0001$) and P:PE ($I = 0.56$, $P < 0.0001$). Correlations with these climate variables were observed at relatively few sites mostly in the northwest part of the study region. This spatial pattern for correlations with prior year growing season variables (data not shown) was similar to that for early growing season water balance variables for the current year, shown in Fig. 4A, B.

Positive growth–climate correlations with prior winter minimum temperature exhibited significant spatial clustering (Moran's $I = 0.305$, $P < 0.001$, Fig. 4D). The strength of this correlation increased from north to south ($\rho = 0.44$, $P = 0.003$) and from northwest to southeast ($\rho = 0.53$, $P < 0.001$). All sites with significant correlations with pWnMnT except one were located in the southern half of the study region. Six of ten sites where a positive association with pWnMnT was observed were in the southern Appalachian Mountains, at elevations 600–1500 m. The other four sites were north and west and at elevations 270–300 m. Stronger positive associations with pWnMnT were spatially associated with warmer winter temperatures (Fig. 5D).

DISCUSSION

The results of growth–climate correlation analyses indicate that radial growth of tulip poplar is most strongly influenced by site water balance during early growing season of the year the annual ring is formed. Similar findings were reported by Martin-Benito and Pederson (2015), D'Orangeville (2018) and Helcoski et al. (2019). Limited published information about the seasonality of tulip poplar radial growth indicates that the majority of radial growth is completed by the end of July, although some growth may continue through August (Jacquart et al. 1992, McLaughlin et al. 2003). Hence, it is reasonable that conditions during May–July would exert the strongest

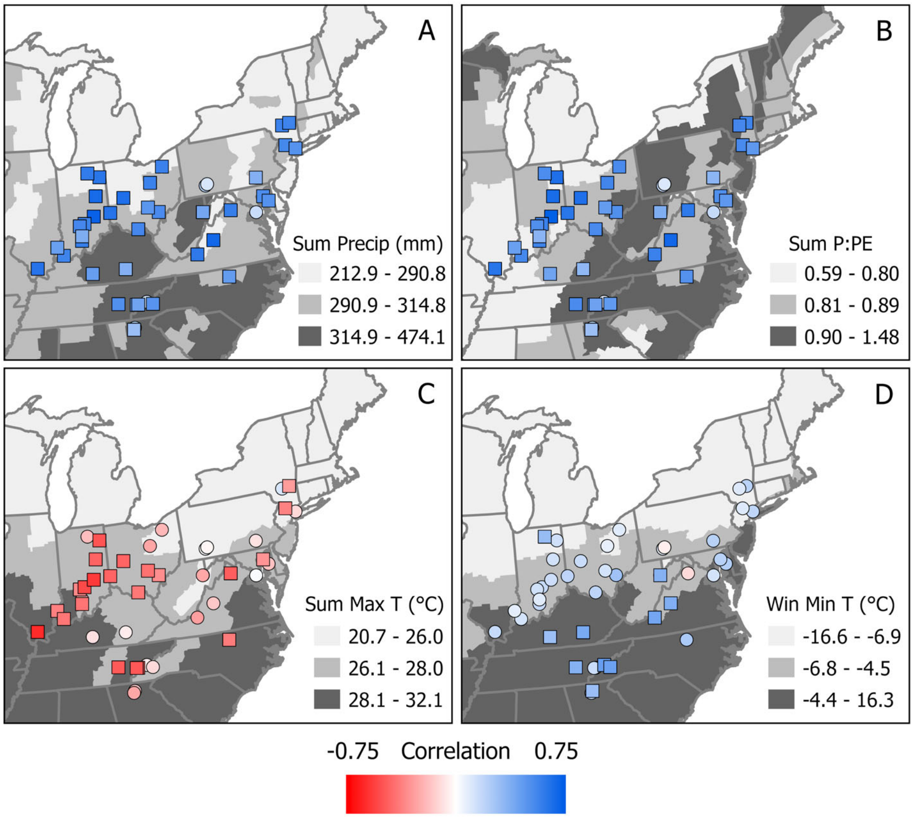

Fig. 4. Spatial patterns in growth–climate correlations for summer precipitation (A), summer P:PE ratio (B), summer maximum temperature (C), and winter minimum temperature (D). Map shading indicates the mean for the climate variable for the period 1930–1980. Plot symbol shape and color indicate the direction and strength of association between radial growth and climate variable. Circles indicate sites where the correlation was not significant ($P \leq 0.05$) and squares where the correlation was significant.

influence on growth increment and conditions after July of the current year would have less or no influence.

Tulip poplar radial growth was correlated with variables associated with drought across almost all 45 sites included in this study, even though many of these sites were located in more mesic environments east of the Appalachian Mountains. In contrast, analyses of growth–climate correlations for oak (*Quercus* spp.) by LeBlanc and Terrell (2009, 2011), LeBlanc and Stahle (2015) and LeBlanc and Berland (2019) using chronologies from some of the same mesic stands where tulip poplar was sampled showed mostly weak or nonsignificant correlations with drought variables. Elliott et al. (2015) also found that diffuse-porous tree species, including tulip poplar, had a greater range of growth response to climate variation than oak species in the same landscape. However, D'Orangeville (2018) found limited evidence for interspecific variation in growth responses to drought among 24 species in eastern North America. The results of the present study indicate that tulip poplar may be equally or more useful for dendroclimatological studies than oak species that have been more widely used in to reconstruct historical drought in eastern North America. A few multi-centennial tulip poplar chronologies from sites in the eastern United States have already used for this purpose (Pederson et al. 2012*a*, *b*, 2013, Maxwell et al. 2015, 2016, Maxwell and Harley 2017).

The phenology of growth–climate correlations for tulip poplar, which has indeterminate apical

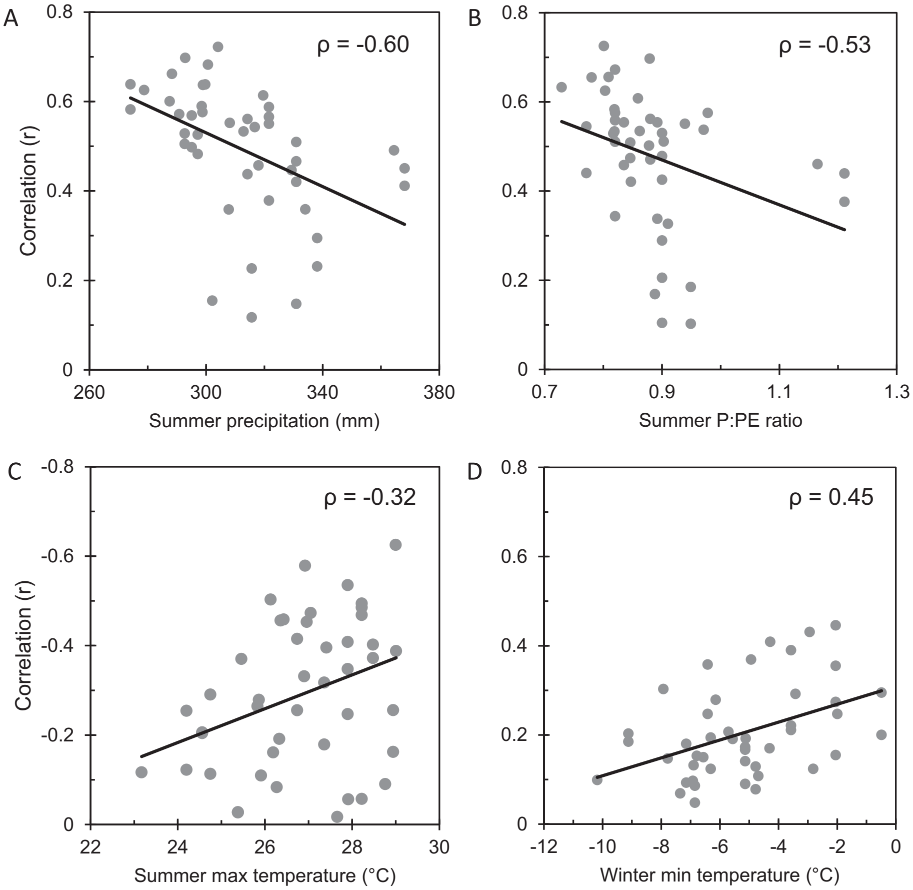

Fig. 5. Growth–climate correlation strength vs. average climate for summer precipitation (A), summer P:PE ratio (B), summer maximum temperature (C), and winter minimum temperature (D). *X*-axis variable is the 51-yr (1930–1980) average for the listed climate variable. *Y*-axis variable is the strength of the correlation between that climate variable and tulip poplar radial growth chronologies. Spearman's rho statistic is listed to quantify the dose–response link between variation in climate and variation in the strength of the growth–climate association.

growth and diffuse-porous wood anatomy, was similar to results obtained for ring-porous oak, hickory (*Carya*), and ash (*Fraxinus*) species, diffuse-porous red maple (*Acer rubrum*), and sugar maple (*A. saccharum*), and many other tree species growing in the eastern United States (Cook et al. 2001, LeBlanc and Terrell 2009, 2011, LeBlanc and Stahle 2015, Martin-Benito and Pederson 2015, Lockwood and LeBlanc 2017, D'Orangeville 2018, Alexander et al. 2019, Helcoski et al. 2019, Maxwell 2019). Most of these other species have determinate apical growth. In all cases, radial growth was positively correlated with May–August precipitation and PDSI and negative correlations with temperature during the same months. Hence, even though tulip poplar may continue apical growth and leaf expansion throughout the growing season, climate in late summer appears to have weak or no influence on radial growth. While some of these studies documented interspecific variation in growth–climate correlations for months during the prior year and spring, these associations were often weaker than those for the current growing season. Where multiple species were sampled from the same stand, the strength of growth–climate correlations was generally higher for tulip poplar compared with other diffuse-porous species (Elliott et al. 2015, Martin-Benito and Pederson 2015, Maxwell 2019). This is particularly true when compared to bigtooth aspen (*Populus grandidentata*), which had a very weak climate response (Maxwell 2019). However, the growth–climate associations of this diffuse-porous species were based on data from a single site, making it difficult to extrapolate to other sites within the species range. Like Zhao et al. (2018), we recommend that future dendroecological research includes a wider diversity of tree species, particularly diffuse-porous species, sampled at a greater number and diversity of sites in eastern North America so as to better characterize growth–climate relationships for hardwood species in this region.

The results of this study indicate that annual water balance variables may be sufficient to model climate effects of drought on growth of tulip poplar, but that seasonal temperature variables should be used to model direct temperature effects on growth. Similar results were observed for most, but not all, oak species studied by LeBlanc and Terrell (2009), LeBlanc and Stahle (2015) and for white ash (Lockwood and LeBlanc 2017). This difference in the phenology of correlations between water balance versus temperature variables is likely related to the capacity of soil to store water, allowing rainfall during some months to support radial growth during later months.

Growth–climate correlations with variables reflecting conditions during the prior year growing season were observed at a number of the study sites, in spite of the fact that temporal autocorrelation was removed from the tree-ring residual chronologies. Late growing season conditions can influence bud formation and starch storage and thereby influence radial growth during the subsequent year, especially for tree species that have performed shoot growth (Kramer and Kozlowski 1979). Dendroecological studies of other species in eastern North America documented correlations with prior growing season climate variables for some species, but not others (LeBlanc and Terrell 2009, 2011, Bishop et al. 2015, LeBlanc and Stahle 2015, Martin-Benito and Pederson 2015). Species with sustained shoot growth, such as tulip poplar, can continue to produce new foliage throughout the growing season (Zimmerman and Brown 1971). However, this capacity to continue leaf production in the latter half of the growing season does not appear to influence current year ring width, since correlations with late summer climate variables were not spatially replicated. However, late-season shoot growth may contribute to starch reserves that support growth the following year, resulting in the correlations with prior growing season climate variables (Kannenberg et al. 2019).

Multiple studies in North America and Europe have observed positive correlations between radial growth of a deciduous tree species and winter temperature variables, but elucidating the biological mechanism for this association requires further study (Pederson et al. 2004, Martin-Benito and Pederson 2015, Rohner et al. 2016, Weigel et al. 2018, Alexander et al. 2019). While positive correlations with winter temperature were not widespread, there was sufficient spatial replication to make mere coincidence an unlikely explanation. Our study found greater evidence for positive correlations with winter temperature at sites near the warmer range limit of the species, while other studies found similar correlations at sites nearer the colder range limit. This variability of winter temperature correlations among studies and among sites within the same study suggests that local site characteristics (Weigel et al. 2018) or subregional conditions (Pederson et al. 2004) may influence tree sensitivity to winter temperature. Possible mechanisms for winter temperature effects on radial growth of dormant deciduous trees during the following growing season include influences on bud burst and leaf-out (Caffarra and Donnelly 2011) or damage to fine roots associated with soil freezing or frost heaving under diminished snowpack (Tierney et al. 2001, Comerford et al. 2013, Reinmann and Templer 2016). Given projections for increased winter temperatures associated with climate change (USGCRP 2017), the association between deciduous tree growth and winter temperature variables is worthy of further investigation.

While some studies have documented coincident temporal variation in climate and tree growth–climate correlations in eastern North America over recent decades, the results of our study did not find a consistent relationship between temporal variation in tulip poplar growth–climate associations and trends in climate variables. Climate has become wetter after 1980 in the northeast United States and parts of the Ohio River Valley (Ficklin et al. 2015), with increased daily rainfall during the growing season between 1990 and 2013 (Bishop and Pederson 2015). Others have reported increased rainfall throughout the northern half of the eastern United States, while drought frequency has increased in the southeastern states (USGCRP 2017). Temporal trends of increasing precipitation and PDSI were also found in the climate data used in the current study. Based on a moving window correlation analysis, Maxwell et al. (2016) and Helcoski et al. (2019) documented weakened correlations between growth and growing season PDSI after 1970 that was consistent across multiple tree species and sites. Maxwell et al. (2016) and Helcoski et al. (2019) concluded that wetter climate conditions after 1970 had resulted in weaker correlations between tree growth and climate variables. The results of the Kalman filter analyses presented here found a similar decrease in the strength of associations with variables related to growing season water balance at some sites. However, at other sites the strength of this association increased in spite of wetter conditions. Additional studies that include multiple sites that span significant spatial climate gradients are needed to better understand how climate change will influence tree growth responses to climate stresses.

Spatial variation in the influence of growing season water balance and temperature variables on radial growth was generally consistent with a spatial climate gradient of decreasing precipitation and P:PE from southeastern to northwestern parts of the species range. The east–west pattern of spatial variation in strength of correlations with early growing season maximum temperature was perpendicular to the north–south spatial gradient for this climate variable. This suggests that the influence of growing season temperature is mediated only indirectly through its effect on site water balance. High summer temperature would be more stressful in the western part of the species range where growing season precipitation and P:PE are lower and droughts are more frequent. Most tree species respond to drought stress by closing leaf stomata to reduce evapotranspiration water loss, which temporarily reduces carbon uptake and photosynthesis. This may also result in irreversible damage to leaves that overheat due to limited evaporative cooling, especially if drought is coincident with above-average temperature (Hamerlynck and Knapp 1996). Tulip poplar often responds to drought stress by prematurely dropping foliage, thereby reducing demand for evapotranspiration (Kramer and Kozlowski 1979). However, this also results in loss of photosynthetic leaf area. The consistent correlation between tulip poplar radial growth and early growing season site water balance variables may be caused in part by foliar damage or leaf loss during droughts that limits subsequent carbon uptake, even if drought conditions were ameliorated by rainfall later in the growing season.

While radial growth of tulip poplar is mostly affected by climate conditions during the early growing season when radial growth occurs, this species may still be vulnerable to projected climate change that could cause more frequent late summer droughts (USGCRP 2017). The correlations with prior growing season climate variables documented here suggest that late summer droughts could affect starch storage or bud set and cause reduced growth during the following growing season (Helcoski et al. 2019, Kannenberg et al. 2019).

Observational correlation studies, such as the study reported, here cannot provide conclusive evidence of cause–effect relationships between variation in climate variables and the growth responses of tree species. However, the spatial replication of the growth–climate correlations observed in this study, the well-documented biological mechanism by which site water balance and temperature affect plant physiology and growth, and the dose-dependent response pattern of increasing strength of correlations along climate gradients of increasingly stressful conditions provide strong evidence that these correlations reflect cause–effect. Hence, we believe that our results provide useful information for those who work to improve the biological realism of forest simulation models.

Iverson (2017) compared projections of climate change effects on abundance of common tree species in central and northeastern regions of the eastern United States among distribution models, process models, and landscape models. While the projections from these very different models were consistent for many tree species, the results for tulip poplar were not. Under the same climate change scenario for the same subregion, some models projected large increases in tulip poplar abundance, while others projected small decreases. Similar mixed results were presented for projected abundance of suitable tulip poplar habitat in Indiana, Illinois, and Missouri (Brandt et al. 2014). None of these model projections addressed the question of how climate change in the next 100 yr will affect existing mature trees.

The results of this dendroecological study provide spatially explicit information about where and to what degree existing tulip poplar populations in the eastern United States may be sensitive to climate change in the twenty-first century. Tulip poplar is sensitive to low soil water availability during the early growing season, especially in the region west of the Appalachian Mountains, but may not suffer direct effects from increasing temperature. Anecdotally, a 1999 drought was associated with widespread mortality of tulip poplar in Indiana, located within this western region (Chaney 2000). Hence, if climate change in the coming decades reduces soil water availability during the growing season, as projected (USGCRP 2017), tulip poplar productivity and mortality in the affected regions will be adversely impacted. Given the abundance and rapid growth of tulip poplar in the eastern United States, these adverse effects could have a substantial impact on forest carbon sequestration in this region.

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LITERATURE CITED

Adams, H. D., G. A. Barron-Gafford, R. L. Minor, A. A. Gardea, L. P. Bentley, D. J. Law, D. D. Breshears, N. G. McDowell, and T. E. Huxman. 2017. Temperature response surfaces for mortality risk of tree species with future drought. Environmental Research Letters 12:115014.

Alexander, M. R., J. K. Pearl, D. A. Bishop, E. R. Cook, K. J. Anchukaitis, and N. Pederson. 2019. The potential to strengthen temperature reconstructions in ecoregions with limited tree line using a multispecies approach. Quaternary Research 92:583–597.

Allen, C., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:1–55.

Anderegg, W., et al. 2015. Tree mortality from drought, insects, and their interactions in a changing climate. New Phytologist 208:674–683.

Anderegg, W., J. Kane, and L. Anderegg. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nature Climate Change 3:30–36.

Bishop, D. A., C. M. Beier, N. Pederson, G. B. Lawrence, J. C. Stella, and T. J. Sullivan. 2015. Regional growth decline of sugar maple (*Acer saccharum*) and its potential causes. Ecosphere 6:179–193.

Bishop, D. A., and N. Pederson. 2015. Regional variation of transient precipitation and rainless day frequency across a subcontinental hydroclimate gradient. Journal of Extreme Events 2:1550007.

Brandt, L., et al. 2014. Central Hardwoods ecosystem vulnerability assessment and synthesis: a report from the Central Hardwoods Climate Change Response Framework project. General Technical Report NRS-124. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America, Volume 2, Hardwoods. Agriculture Handbook 654, United States Department of Agriculture, Forest Service, Superintendent of Documents, U.S. Government Printing Office, Washington, D.C., USA.

Caffarra, A., and A. Donnelly. 2011. The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. International Journal of Biometeorology 55:711–721.

Canham, C. D., and R. Q. Thomas. 2010. Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America. Ecology 91:3433–3440.

Chaney, W. R. 2000. Yellow poplar and drought. Indiana Woodland Steward 9. http://woodlandsteward.squarespace.com/storage/past-issues/yellowpo.htm

Charney, N. D., F. Babst, B. Poulter, S. Record, V. M. Trouet, D. Frank, B. J. Enquist, and M. E. Evans. 2016. Observed forest sensitivity to climate implies large changes in 21st century North American forest growth. Ecology Letters 19:1119–1128.

Choat, B., et al. 2012. Global convergence in the vulnerability of forests to drought. Nature 491:752–755.

Comerford, D. P., P. G. Schaberg, P. H. Templer, A. M. Socci, J. L. Campbell, and K. F. Wallin. 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. Oecologia 171:261–269.

Cook, B. I., J. E. Smerdon, R. Seager, and S. Coats. 2014. Global warming and 21st century drying. Climate Dynamics 41:501–516.

Cook, E. R. 1985. A time series analysis approach to tree ring standardization. Dissertation. University of Arizona, Tucson, Arizona, USA.

Cook, E. R., J. S. Glitzenstein, P. J. Krusic, and P. A. Harcombe. 2001. Identifying functional groups of trees in west Gulf Coast forests (USA): a tree-ring approach. Ecological Applications 11:883–903.

Cook, E. R., and A. H. Johnson. 1989. Climate change and forest decline: a review of the red spruce case. Water Air and Soil Pollution 48:127–140.

Currie, D. J., and V. Paquin. 1987. Large-scale biogeographical patterns of species richness of trees. Nature 329:326–327.

Dale, M. R. T., and M. J. Fortin. 2014. Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge, UK.

D'Orangeville, L., et al. 2018. Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. Global Change Biology 24:2339–2351.

Dyer, J. M. 2006. Revisiting the deciduous forests of eastern North America. BioScience 56:341–352.

Elliott, K., C. Miniat, N. Pederson, and S. Laseter. 2015. Forest tree growth response to hydroclimate variability in the southern Appalachians. Global Change Biology 21:4627–4641.

Fan, Z., X. Fan, M. K. Crosby, W. K. Moser, H. He, M. A. Spetich, and S. R. Shifley. 2012. Spatio-temporal trends of oak decline and mortality under periodic regional drought in the Ozark Highlands of Arkansas and Missouri. Forests 3:614–631.

Ficklin, D. L., J. R. Maxwell, S. L. Letsinger, and H. Gholizadeh. 2015. A climatic deconstruction of recent drought trends in the United States. Environmental Research Letters 10:044009.

Hamerlynck, E., and A. K. Knapp. 1996. Photosynthetic and stomatal responses to high temperature and light in two oaks at the western limit of their range. Tree Physiology 16:557–565.

Helcoski, R., A. J. Tepley, N. Pederson, J. C. McGarvey, V. Meakem, V. Herrmann, J. R. Thompson, and K. J. Anderson-Teixeira. 2019. Growing season moisture drives interannual variation in woody productivity of a temperate deciduous forest. New Phytologist 223:1204–1216.

Holmes, R. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43:69–75.

ITRDB. 2018. International Tree-Ring Data Bank, IGBP PAGES/World Data Center for Paleoclimatology. NOAA National Climate Data Center, Boulder, Colorado, USA. https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring

Iverson, L. R., et al. 2017. Multi-model comparison on the effects of climate change on tree species in the eastern U.S.: results from an enhanced niche model and process-based ecosystem and landscape models. Landscape Ecology 32:1327–1346

Jacquart, E. M., T. V. Armentano, and A. L. Spingarn. 1992. Spatial and temporal tree responses to water stress in an old-growth deciduous forest. American Midland Naturalist 127:158–171.

Kalman, R. E. 1960. A new approach to linear filtering and prediction problems. Journal of Fluid Engineering 82:35–45.

Kannenberg, S. A., J. T. Maxwell, N. Pederson, L. D'Orangeville, D. L. Ficklin, and R. P. Phillips. 2019. Drought legacies are dependent on water table depth, wood anatomy and drought timing across the eastern US. Ecology Letters 22:119–127.

Keith, H., B. G. Mackey, and D. B. Lindenmayer. 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. Proceedings National Academy of Sciences 106:11635–11640.

Kramer, P. J., and T. T. Kozlowski. 1979. physiology of woody plants. Academic Press, Cambridge, Massachusetts, USA.

LeBlanc, D. C. 1993. Temporal and spatial variation of oak growth–climate relationships along a pollution gradient in the Midwestern United States. Canadian Journal of Forest Research 23:772–782.

LeBlanc, D. C., and A. Berland. 2019. Spatial variation in oak (*Quercus* spp.) radial growth responses to drought stress in eastern North America. Canadian Journal of Forest Research 48:986–993.

LeBlanc, D. C., and D. W. Stahle. 2015. Radial growth responses of four oak species to climate in eastern and central North America. Canadian Journal of Forest Research 45:793–804.

LeBlanc, D. C., and M. Terrell. 2001. Dendroclimatic analyses using Thornthwaite–Mather-type evapotranspiration models: a bridge between dendroecology and forest simulation models. Tree-Ring Research 57:55–66.

LeBlanc, D. C., and M. A. Terrell. 2009. Radial growth response of white oak (*Quercus alba*) to climate in Eastern North America. Canadian Journal of Forest Research 39:2180–2192.

LeBlanc, D. C., and M. A. Terrell. 2011. Comparison of growth-climate relationships between white oak and northern red oak across eastern North America. Canadian Journal of Forest Research 41:1936–1947.

Lockwood, B. R., and D. C. LeBlanc. 2017. Radial growth-climate relationships of white ash (*Fraxinus americana* L.) in the eastern United States. Journal of the Torrey Botanical Society 144:267–279.

Manion, P. D. 1990. Tree disease concepts. Second edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Martin-Benito, D., and N. Pederson. 2015. Convergence in drought stress, but a divergence of climatic drivers across a latitudinal gradient in a temperate broadleaf forest. Journal of Biogeography 42:925–937.

Maxwell, J. T., et al. 2019. Higher CO_2 concentrations and lower acidic deposition have not changed drought responses in tree growth but do influence iWUE in hardwood trees in the Midwestern USA. Journal of Geophysical Research: Biogeosciences 124:3798–3813.

Maxwell, J. T., and G. L. Harley. 2017. Increased tree-ring network density reveals more precise estimations of sub-regional hydroclimate variability and climate dynamics in the Midwest, USA. Climate Dynamics 49:1479–1493.

Maxwell, J. T., G. L. Harley, and T. J. Matheus. 2015. Dendroclimatic reconstructions from multiple co-occurring species: a case study from an old-growth deciduous forest in Indiana, USA. International Journal of Climatology 35:860–870.

Maxwell, J. T., G. L. Harley, and S. M. Robeson. 2016. On the declining relationship between tree growth and climate in the Midwest United States: the fading drought signal. Climatic Change 138:127–142.

McLaughlin, S., D. Downing, T. Blasing, B. Jackson, D. Pack, D. Duvick, L. Mann, and T. Doyle. 1986. FORAST Data Base Documentation. Environmental Sciences Division Publication No. 4895, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

McLaughlin, S. B., S. D. Wullschleger, and M. Nosal. 2003. Diurnal and seasonal changes in stem increment and water use by yellow poplar trees in response to environmental stress. Tree Physiology 23:1125–1136.

NCDC. 2018. National Climate Data Center. https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp

Pederson, N., A. R. Bell, E. R. Cook, U. Lall, N. Devineni, R. Seager, K. Eggleston, and K. P. Vranes. 2013. Is an epic pluvial masking the water insecurity of the Greater New York City region? Journal of Climate 26:1339–1354.

Pederson, N., K. Tackett, R. W. McEwan, S. Clark, A. Cooper, G. Brosi, R. Eaton, and R. D. Stockwell. 2012*a*. Long-term drought sensitivity of trees in second-growth forests in a humid region. Canadian Journal of Forest Research 42:1837–1850.

Pederson, N., et al. 2012*b*. A long-term perspective on a modern drought in the American Southeast. Environmental Research Letters 7:014034.

Pederson, N., E. R. Cook, G. C. Jacoby, D. M. Peteet, and K. L. Griffin. 2004. The influence of winter temperatures on the annual radial growth of six northern range margin tree species. Dendrochronologia 22:7–29.

Reinmann, A. B., and P. H. Templer. 2016. Reduced winter snowpack and greater soil frost reduce live root biomass and stimulate radial growth and stem respiration of red maple (*Acer rubrum)* trees in a mixed-hardwood forest. Ecosystems 19:129–141.

Rohner, B., P. Weber, and E. Thűrig. 2016. Bridging tree rings and forest inventories: How climate effects on spruce and beech growth aggregate over time. Forest Ecology and Management 360:159–169.

Tierney, G. L., T. J. Fahey, P. M. Groffman, J. P. Hardy, R. D. Fitzhugh, and C. T. Driscoll. 2001. Soil freezing alters fine root dynamics in a northern hardwood forest. Biogeochemistry 56:175–190.

USGCRP. 2017. Climate Science Special Report: Fourth National Climate Assessment, Volume I. *In* Wuebbles, D. J., D. W. Fahey, K. A. Hibbard, D. J. Dokken, B. C. Stewart, and T. K. Maycock, editors. U.S. Global Change Research Program, Washington, D.C., USA.

Visser, H., U. Büntgen, R. D'Arrigo, and A. C. Petersen. 2010. Detecting instabilities in tree-ring proxy calibration. Climate Past 6:367–377.

Weigel, R., L. Muffler, M. Klisz, J. Kreyling, M. van der Maaten-Theunissen, M. Wilmking, and E. van der Maaten. 2018. Winter matters: Sensitivity to winter climate and cold events increases towards the cold distribution margin of European beech (*Fagus sylvatica* L.). Journal of Biogeography 45:2779–2790.

Williams, A. P., et al. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3:292–297.

Wood, J. D., B. O. Knapp, R. M. Muzika, M. C. Stambaugh, and L. Gu. 2018. The importance of drought–pathogen interactions in driving oak mortality events in the Ozark Border Region. Environmental Research Letters 13:015004.

Zhao, S., N. Pederson, L. D'Orangeville, J. HilleRisLambers, E. Boose, C. Penone, B. Bauer, Y. Jiang, and R. D. Manzanedo. 2018. The International Tree-Ring Data Bank (ITRDB) revisited: data availability and global ecological representativity. Journal of Biogeography 46:355–368.

Zimmerman, M. H., and C. L. Brown. 1971. Trees structure and function. Springer-Verlag, New York, New York, USA.

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